

# Testing the divergent adaptation of two congeneric tree species on a rainfall gradient using eco-physio-morphological traits

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## Abstract

In tropical Africa, evidence of widely distributed genera transcending biomes or habitat boundaries has been reported. The evolutionary processes that allowed these lineages to disperse and adapt into new environments are far from being resolved. To better understand these processes, we propose an integrated approach, based on the eco-physio-morphological traits of two sister species with adjacent distributions along a rainfall gradient. We used wood anatomical traits, plant hydraulics (vulnerability to cavitation, wood volumetric water content, and hydraulic capacitance), and growth data from the natural habitat, in a common garden, to compare species with known phylogeny, very similar morphologically, but occupying contrasting habitats: *Erythrophleum ivorense* (wet forest) and *Erythrophleum suaveolens* (moist forest and forest gallery). We identified some slight differences in wood anatomical traits between the two species associated with strong differences in hydraulics, growth, and overall species distribution. The moist forest species, *E. suaveolens*, had narrower vessels and intervessel pits, and higher vessel cell-wall reinforcement than *E. ivorense*. These traits allow a high resistance to cavitation and a continuous internal water supply of the xylem during water shortage, allowing a higher fitness during drought periods, but limiting growth. Our results confirm a trade-off between drought tolerance and growth, controlled by subtle adaptations in wood traits, as a key mechanism leading to the niche partitioning between the two *Erythrophleum* species. The generality of this trade-off and its importance in the diversification of the African tree flora remains to be tested. Our integrated eco-physio-morpho approach could be the way forward.

Abstract in French is available with online material.

## KEYWORDS

African tropical trees, cavitation, diversification, growth, hydraulic capacitance, niche partitioning, sister species, wood anatomy

## 1 | INTRODUCTION

In tropical Africa, geographical patterns of plant diversity and endemism have been frequently reported (Linder, 2001; Sosef et al., 2017) and related to rainfall gradients (Linder, 2001; O'Brien, 1998). While some African genera have been associated with specific biomes (Linder, 2014), evidence of widely distributed genera transcending biome or habitat boundaries has also been reported for herbaceous plants (for palms species, see Blach-Overgaard, Svenning, Dransfield, Greve & Balslev, 2010, or for the *Coccinia* genus Holstein & Renner, 2011) and for trees (see the early work of White, 1978 on *Diospyros*, and the more recent genetics studies of Donkpegan, 2017 on *Azelia*, and Tosso, 2018 on *Guibourtia*). The evolutionary processes that allowed lineages to disperse and adapt into new environments are far from being resolved and probably yield multiple answers. While a diversity of approaches, at different spatial and phylogenetic scales, can provide complementary insights, detailed analyses of resolved clades are needed to build robust generalizations (Donoghue & Edwards, 2014).

Niche evolution along rainfall gradients suggests adaptation to drought, and for trees, two extreme drought resistance strategies are generally recognized: desiccation delay and desiccation tolerance (Tyree, Engelbrecht, Vargas & Kursar, 2003). The desiccation delay strategy involves traits that increase access to water and reduce water loss, including deep roots, early stomatal closure, low cuticular conductance, water storage in plant organs, osmotic adjustments, and leaf shedding (Lachenbruch, Moore & Evans, 2011; Santiago, Bonal, De Guzman & Ávila-Lovera, 2016; Westoby, Falster, Moles, Vesk & Wright, 2002). In contrast, the desiccation tolerance strategy is promoted by physiological traits that sustain continued water transport, gas exchange, or cell survival at low water content (WC) and low water potential ( $\Psi$ ), such as resistance of xylem to embolism formation, and the ability of cells to remain alive at low WC and  $\Psi$ .

Sensitivity of xylem to embolism represents an important constraint on tree functioning and survival during drought (Brodribb & Cochard, 2009; O'Brien et al., 2017; Urli et al., 2013). Quantifying the tension under which xylem embolizes has been the principal approach to characterize drought resistance in woody species (Choat, Sack & Holbrook, 2007; Santiago et al., 2016). More recently, hydraulic capacitance, that is, stored water in stems and plant organs that can temporarily supply the transpiration stream and protect xylem from precipitous drops in water potential, has emerged as one of the most important aspects of tree hydraulics for understanding the actual risk of cavitation (Epila, Maes, et al., 2017; Scholz, Phillips, Bucci, Meinzer & Goldstein, 2011; Vergeynst, Sause, Hamstad & Steppe, 2015). Tropical trees with high capacitance have been shown to survive drought even with low cavitation resistance, because of the buffering role of stored water and the lower risk of reaching the xylem tension that causes hydraulic failure (Epila, Maes, et al., 2017; Meinzer, James & Goldstein, 2004; Sperry, Meinzer & McCulloh, 2008; Wolfe, 2017). In the tropics, the paucity of data on hydraulics has to be noted

(see Choat et al., 2007 for available hydraulic data), specifically for African tree species (but see Epila, Maes, et al., 2017 for *Maesopsis eminii*).

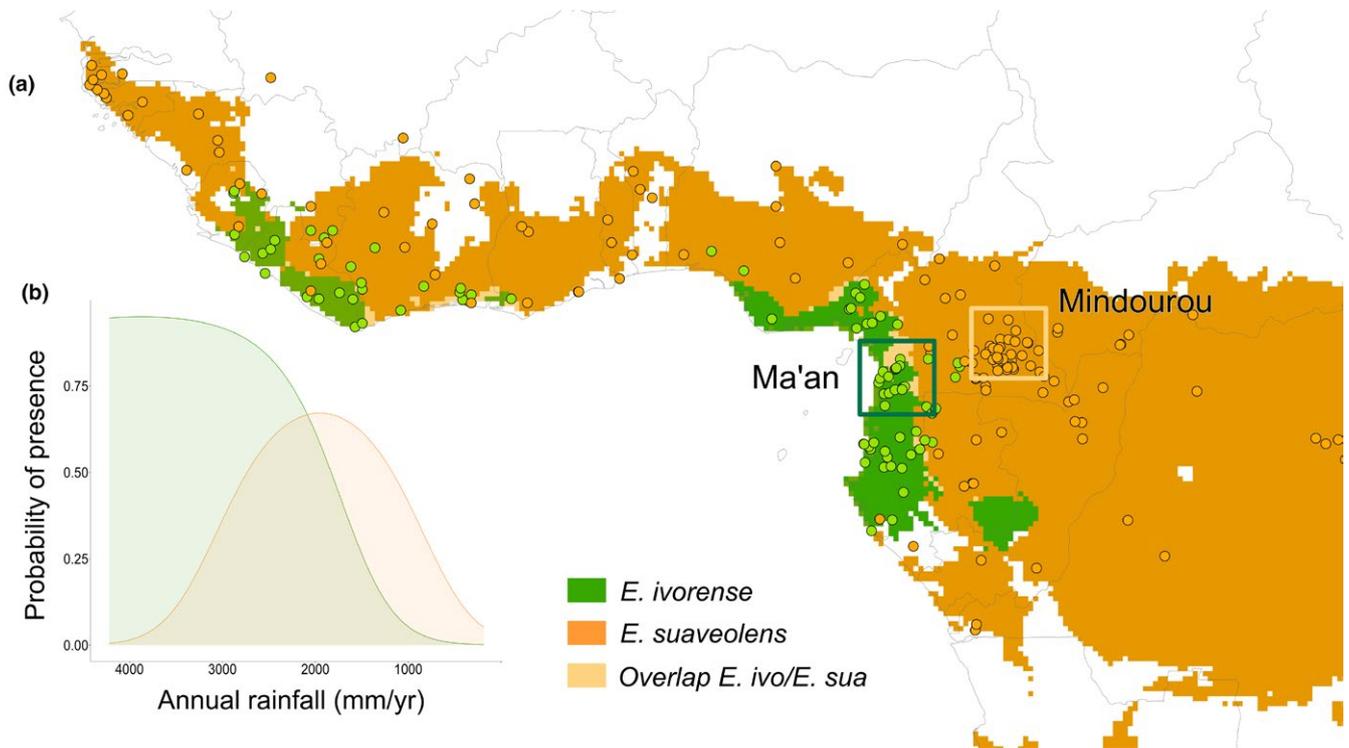
Differential adaptation to drought, and specifically hydraulics, suggests structural differences in wood anatomy. Wood anatomy indeed directly relates to conductivity, xylem safety, and hydraulic capacitance (Beeckman, 2016; Borchert & Pockman, 2005; Lachenbruch & McCulloh, 2014). Angiosperms with wide vessels have higher water transport efficiency, but are more vulnerable to cavitation (Gleason et al., 2016; Zanne et al., 2013). However, vessel size and abundance only partially explain conductivity and xylem safety (Choat, Cobb & Jansen, 2008). The passage of sap flow through the intervessel pits, the vessel cell-wall reinforcement, and the connectivity of the conduit network are at least as important as conduit size and abundance. In addition, the high water storage capacity of parenchyma of the secondary xylem is expected to contribute to hydraulic capacitance together with the conduits (Anderegg & Meinzer, 2015; Epila et al., 2017; Morris & Jansen, 2016).

In this study, we examined how tree species evolved on a rainfall gradient with an integrated eco-physio-morphological approach. Our case study, the *Erythrophleum* genus in Africa, belongs to the Fabaceae, one of the most abundant families in tropical forests. We specifically studied *Erythrophleum ivorense* and *E. suaveolens*, two sister species, morphologically similar, often confused in the field, and traded under the same commercial name, Tali. The species, however, occupy very different areas in Upper and Lower Guinea (as revealed by genetics: Duminil, Heuertz, Doucet, et al., 2010), and contrasting forest types and rainfall conditions, with little overlap (Figure 1). *E. ivorense* is restricted to coastal wet evergreen forests in the Gulf of Guinea. In contrast, *E. suaveolens* is widespread across tropical Africa, encompassing moist forests of the Guineo-Congolian Region and savannas of the Sudanian and Zambebian Regions (White, 1983). Here, we examined between-species variation in tree hydraulics including vulnerability to cavitation, wood water content, and capacitance, and we determined the underlying wood traits including especially vessel-associated traits. Growth and life-history traits were also examined. A common garden was specifically used to test whether differences in growth and wood traits are maintained under the same environment.

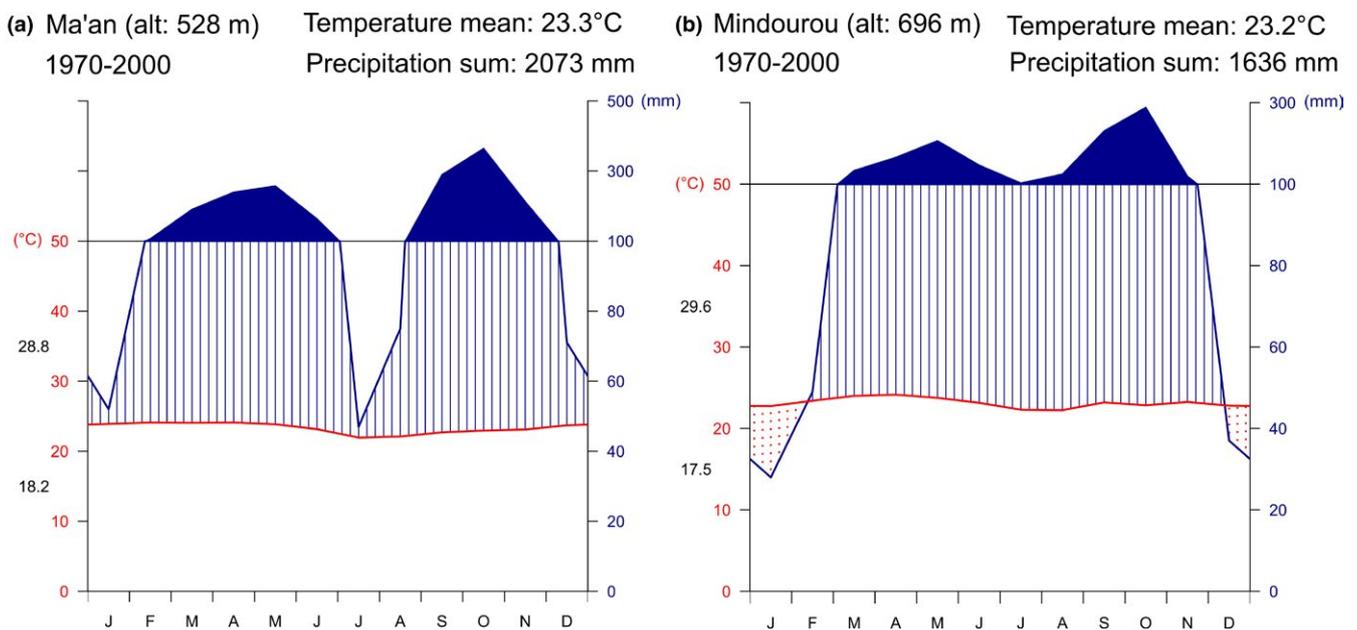
## 2 | METHODS

### 2.1 | Study sites

Data and samples were collected in two sites in southern Cameroon: the Ma'an site, east of the Campo-Ma'an National Park, natural habitat of *E. ivorense* (around 2°22'N and 10°37'E) and the Mindourou site, east of the Dja Faunal reserve, natural habitat of *E. suaveolens* (around 3°33'N and 13°14'E, Figure 1). Forests in the Ma'an site are assigned to Wet Central Africa (Fayolle et al., 2014, hereinafter designated as "wet forest") and correspond to lowland evergreen forests (Letouzey, 1985). The annual rainfall is up to 2,070 mm with two periods of maximum rainfall separated with drier periods without



**FIGURE 1** Species distribution and study sites. Potential distribution in Upper and Lower Guinea (a) and response curve (probability of presence) along the rainfall gradient (b) of the two sister species *Erythropileum ivorense* (in green) and *E. suaveolens* (in orange). The average rainfall has been extracted from “bioclim” data (BIO12, Hijmans et al., 2005) and corresponds to the average of the rainfall measured over a 30-year period (from 1970 to 2000). Note that the distribution of *E. suaveolens* is much larger across southern and eastern Africa, but genetic information is lacking (Duminil, Heuertz & Hardy, 2010). The location of the two study sites Ma'an and Mindourou in Cameroon, corresponding to the natural habitat of *E. ivorense* and *E. suaveolens*, respectively, is indicated on the map (colored squares). The common garden experiment was set up at the Mindourou site, that is, in the natural habitat of *E. suaveolens*. The occurrence data used to model the distribution of the species overlaid on the map. The potential distributions and the response curves result from species-specific distribution modeling. See Supporting Information Appendix S1 for a description of the methods we used



**FIGURE 2** Climate diagrams. Walter–Lieth climate diagram of monthly average temperature (red solid line) and precipitation (blue solid line) for the Ma'an site (a), natural habitat of *E. ivorense*, and the Mindourou site (b), natural habitat of *E. suaveolens*. The diagrams were constructed with the “Wordclim” data (Hijmans et al., 2005)

real water deficit (monthly precipitation no <45 mm, Figure 2). The mean annual temperature is 23.3°C (Hijmans et al., 2005). Forests in the Mindourou site are assigned to Moist Central Africa (Fayolle et al., 2014, hereinafter designated as "moist forest") and have been previously described as a transition type between the evergreen and the semi-deciduous forests with a canopy dominated by species of the Meliaceae, Malvaceae, and Ulmaceae families indicating a strong floristic affinity with the semi-deciduous forests (Letouzey, 1985). The annual rainfall is up to 1640 mm with a pronounced dry season of almost three months (December to February), and the mean annual temperature is 23.2°C (Figure 2). In both sites, the topography is undulating, with elevation varying between 600 and 800 m, and between 500 and 650 m, in the Ma'an and Mindourou sites, respectively. The geological substrate consists of volcanic intrusions and metamorphic rocks, and soils are generally attributed to Ferralsols (Jones et al., 2013).

In the Mindourou site, the two study species were also grown in a common garden. Seeds were collected from multiple mother trees in north-west Gabon for *E. ivorens* and from four provenances for *E. suaveolens*, but we restricted our analyses to the provenance close to the Mindourou site. Juveniles were raised in a nursery for six months prior to plantation in 2008. The common garden experiment followed a randomized block design (20 randomized blocks, with 20 trees per block). Each block contained a single offspring per mother tree, planted at distances of 10 m.

## 2.2 | Field sampling

In the natural habitat, branch and stem samples were collected during daytime in March 2016 on felled trees (day of year (DOY) 71 and 72 for *E. ivorens* ( $n = 9$ ) and DOY 90 and 92 for *E. suaveolens* ( $n = 5$ )). Average height ( $\pm SD$ ) was 33.00 ( $\pm 4.19$ ) m for *E. ivorens* in Ma'an and 34.08 ( $\pm 1.42$ ) m for *E. suaveolens* in Mindourou, and these trees can be considered as mature trees.

In the common garden, branch samples were collected during March 2015 on *E. ivorens* ( $n = 8$ ) and *E. suaveolens* ( $n = 7$ , DOY 68–72). We selected individuals with the best growth rate, no liana infestation, and crown dieback since 2008. Average height ( $\pm SD$ ) was 12.25 ( $\pm 3.15$ ) m for *E. ivorens* and 9.70 ( $\pm 3.53$ ) m for *E. suaveolens*, and these 7-year-old trees can be considered as juvenile trees.

To quantify hydraulic traits, branches from the natural habitat were cut under water. The cut end was put immediately into a small vial filled with water, and the branch was enclosed in a wet and opaque plastic bag. The branch samples were conserved in a cool box until measurements. These precautions were taken to keep the branch segments in a hydraulic equilibrium state from the field to the laboratory. Excised branches of *E. ivorens* and *E. suaveolens* were transported on DOY 75 and DOY 97, respectively, to the Laboratory of Plant Ecology, Ghent University (Belgium).

To quantify wood traits, branch samples were collected between 10 and 20 cm from the apex, and stem samples were collected at breast height (1.30 m). Samples were stored in 50% ethanol until

measurements in laboratory of the Wood Biology Service of the Royal Museum for Central Africa (Belgium).

## 2.3 | Hydraulic traits

In the laboratory, branches from three individuals (out of all the branches sampled) per species were selected on uniformity in length (average ( $\pm SD$ ) was 80  $\pm$  11 cm for *E. ivorens* and 81  $\pm$  4.1 cm for *E. suaveolens*) and diameter (9.2  $\pm$  1.8 mm for *E. ivorens*; 8.7  $\pm$  0.8 mm for *E. suaveolens*) to minimize statistical sampling variability. Branches were analyzed from DOY 75–76 for *E. ivorens* and from DOY 97–100 for *E. suaveolens*.

During the preparation steps, the experimental room was darkened with an artificial green light to diminish photosynthesis and transpiration (De Baerdemaeker, Salomón, De Roo & Steppe, 2017). For each species, three branches were placed in a custom-built holder and equipped with a broadband point-contact acoustic emission (AE) sensor (KRNBB-PC, KRN Services, Richland, WA, USA) and a dendrometer (DD-S, Ecomatik, Dachau, Germany). Three other branches were placed on continuous weighing scales after removing the leaves and covering the created wounds with petroleum jelly. For AE-selected branches, all the leaves were wrapped in aluminum foil to equalize the dehydration procedure. Wrapping leaves in aluminum foil allowed the determination of stem water potential ( $\psi$ , MPa) with the pressure chamber (PMS Instrument Company, Corvallis, OR, USA). The AE sensor and the dendrometer were installed directly onto the xylem surface by removing two sections of bark (1.5  $\times$  0.5 mm). To avoid evaporation and provide good acoustic contact, vacuum grease was applied between the AE sensor tip and the xylem surface, while petroleum jelly was smeared against the exposed section for the dendrometer to similarly avoid evaporation. At the end of the preparation steps, the water-filled vial was removed from both sets of branches. The first measure of stem water potential was close to zero indicating no sign of premature drought stress, and no trace of gel or tylose clogging of vessels was detected on optical micrographs.

Collected AE signals were used to construct an acoustic vulnerability curve ( $VC_{AE}$ , Vergeynst, Dierick, Bogaerts, Cnudde & Steppe, 2015; Vergeynst, Sause, et al., 2015; De Baerdemaeker et al., 2017). The AE signals were cumulated over the measurement period and averaged over 5 minutes. The endpoint of the  $VC_{AE}$  was based on the local maximum in the third derivative, following the strongest decrease in the first derivative. Cumulative acoustic emissions were then rescaled between zero and the defined endpoint to obtain a relative percentage of cavitation-related AE (%). The continuous water potential x-axis of the  $VC_{AE}$  was obtained from a segmented linear regression relation between point measurements of xylem water potential and xylem shrinkage monitored by the dendrometers (De Baerdemaeker et al., 2017). Thresholds corresponding to the onset of embolism ( $AE_{12}$ ), 50% cavitation-related AE ( $AE_{50}$ ), full embolism ( $AE_{88}$ ), and endpoint of the  $VC_{AE}$  ( $AE_{100}$ ) were assessed as well (De Baerdemaeker et al., 2017).

In order to normalize weight loss data to wood volumetric water content (VWC,  $\text{kg}/\text{m}^3$ ), ~5 cm wood samples were taken at the start and the end of the dehydration experiment of both sets of branches. Diameter, length, and weight were measured. Each sample was then oven-dried ( $100^\circ\text{C}$ ) till constant mass, after which the respective quantities were re-measured. Because water potential data are only obtained from the AE branches, the AE wood samples are used to calculate VWC by re-scaling weight loss data between initial and final water content of the samples (Vergeynst, Dierick, et al., 2015). Samples collected from the scale-selected branches were used as a reference to validate that both sets of branches dehydrated in a similar manner. The resulting desorption curve is obtained by plotting wood VWC against the continuous  $\Psi$  axis. Within this curve, three regions of interest are determined based on three defined breakpoints, calculated via the Segmented package (Muggeo, 2008) in the R software (R Core Team 2016). The zone between the first and second breakpoints is known as the initial phase or capillary water phase. The zone between the second and third breakpoints is the elastic phase or phase I, and the zone after the third breakpoint till the  $\text{AE}_{100}$  is the inelastic phase or phase II (Epila, Baerdemaeker, et al., 2017; Vergeynst, Dierick, et al., 2015). The hydraulic capacitance, defined as the amount of water released from the tissue into the xylem per unit decrease in  $\Psi$ , is then calculated for the distinct phases as the slope of the linear regression between VWC and  $\Psi$  (Vergeynst, Dierick, et al., 2015).

Acoustic vulnerability curves and desorption curves were averaged between the different samples.  $\text{VC}_{\text{AE}5}$  are fitted with the *smooth.spline* function in the stats package.

## 2.4 | Wood traits

On branch and stem samples, thin transversal and tangential sections of  $16\ \mu\text{m}$  thickness were cut with a semi-automated microtome (Microm HM 440 E, GMI, Ramsey, MN, USA). The sections were stained in Safranin/Alcian blue mixture, dehydrated in an ethanol series (50%, 75%, 96%), and mounted in Euparal. Sections were transformed into images using an automated OLYMPUS BX60 microscope with a motorized positioning stage (Märzhäuser GmbH & Co. KG, In der Murch 15, 35579 Wetzlar, Germany).

Transverse sections were used to measure tangential vessel diameter, vessel density, and vessel grouping index (ratio of total number of vessels to total number of vessel groupings; Scholz, Klepsch, Karimi & Jansen, 2013). We also quantified the proportion of vessel lumen, fiber, and axial and radial parenchyma. On branch sections, these measurements were done on  $0.16\ \text{mm}^2$  quadrats systematically distributed from the pith to the bark, in order to include radial variation in wood traits. For stem sections, measurements were done on two quadrats of  $9.40\ \text{mm}^2$ . Intervessel wall thickness and fiber wall thickness (measured as the double wall between two adjacent fibers) were also measured at higher magnification. Conduit wall reinforcement was calculated by determining the wall thickness ( $t$ ) to conduit wall span ( $b$ ) ratio  $(t/b)_h^2$  as described by Hacke, Sperry, Pockman, Davis, and

McCulloh (2001). On tangential sections, we measured the horizontal pit membrane diameter at its widest point (sensu Scholz et al., 2013) but only for branch samples from natural habitat. Images were processed with ImageJ 1.47v software.

To test for between-species differences in wood traits, we used linear mixed models fitted with the lme4 R package (Pinheiro, Bates, DebRoy & Sarkar, 2017). Random effects were included in the models to account for individual variability. The best model for each wood trait was selected based on the Akaike information criterion (AIC). We first identified the best random structure and then the best fixed structure following Zuur, Ieno, Walker, Saveliev and Smith (2009). For the stem samples, the full model estimated wood trait ( $WT$ ) of the individuals ( $i$ ) belonging to each species ( $sp$ ), with a random intercept ( $\alpha$ , Equation 1). For the branch samples, except for the fiber wall thickness, the conduit wall reinforcement and the pit membrane diameter for which the Equation 1 has been used, the effect of the distance to the pith ( $dist$ ) and a random slope ( $\beta$ ) have been added in order to consider radial variation in wood anatomy (Equation 2).

$$WT_{i,sp} = a_{sp} + \alpha_{i,sp} + \varepsilon_{i,sp} \quad (1)$$

$$WT_{i,sp} = a_{sp} + b_{sp} \times dist + \alpha_{i,sp} + \beta_{i,sp} \times dist + \varepsilon_{i,sp} \quad (2)$$

with  $a_{sp}$  and  $b_{sp}$  as fixed parameters,  $\alpha_{i,sp}$  and  $\beta_{i,sp}$  as random parameters, and  $\varepsilon_{i,sp}$  as the random error.

## 2.5 | Growth

In the natural habitat of the two species, diameter was monitored yearly since 2013 on a large number of trees covering the species diameter range (*E. ivorens*  $n = 46$ , *E. suaveolens*  $n = 192$ ). The monitoring of tree growth was done on permanent transects in unlogged forest. The diameter measurements were done at breast height (1.30 m). For trees with stem irregularities at breast height, the point of measurement was raised 1 m above the deformations. The diameter was measured with a tape to the nearest millimeter, and a permanent mark was placed on tree trunk to ensure that diameter was monitored every year at the same height. Annual diameter increment was calculated over a 3- to 4-year period. Average initial diameter ( $\pm SD$ ) was  $61.64\ \text{cm}$  ( $\pm 24.01$ ) for *E. ivorens* and  $64.03\ \text{cm}$  ( $\pm 26.70$ ) for *E. suaveolens*.

In the common garden experiment, diameter was monitored yearly (*E. ivorens*  $n = 76$ , *E. suaveolens*  $n = 167$ ). The DBH was measured with a tape to the nearest millimeter, and a permanent mark was placed on tree trunk to ensure that diameter was monitored every year at the same height. Annual diameter increment was calculated since 2010 over a 4-year period. Average initial diameter ( $\pm SD$ ) was  $29.32\ \text{cm}$  ( $\pm 10.36$ ) for *E. ivorens* and  $24.55\ \text{cm}$  ( $\pm 8.24$ ) for *E. suaveolens*.

Between-species differences in growth have been analyzed with one-way ANOVA. To account for the ontogenic variation in growth (Hérault et al., 2011), growth differences in the natural habitat were also examined separately for each 20 cm diameter class. This was preferred to the relative growth rate to account for the nonlinear relationship between growth and size (Hérault et al., 2011).

## 2.6 | Life-history traits

More general traits such as wood density, light requirement, and seed mass were examined. Basic wood density was extracted from the Global Wood Density Database (Zanne et al., 2009) and also measured on branch samples (oven dry mass/green volume, volume was estimated assuming a cylindrical form). Light requirement and seed mass were derived from observations and samples collected in the natural habitat of the species.

To quantify the light requirement at juvenile and mature stages, crown exposure (CE) to light was visually estimated for *E. ivorens* ( $n = 189$  trees covering the species diameter range) and *E. suaveolens* ( $n = 295$ ), following Poorter and Kitajima (2007). The CE varies between 1, for understory trees that do not receive any direct light, and 5 for emergent trees fully exposed to light. The CE was related to tree diameter using a multinomial logistic regression (Sheil, Salim, Chave, Vanclay & Hawthorne, 2006), and the CE at a diameter of 10 cm ( $CE_{juv}$ ) was estimated.

Seed mass was measured on dry seeds collected on well-spaced mother trees (27 seeds from four mother trees for *E. ivorens* and 21 seeds from four trees for *E. suaveolens*). The seeds were dried at 80°C for at least 48 hr following the standardized protocol proposed by Cornelissen et al. (2003).

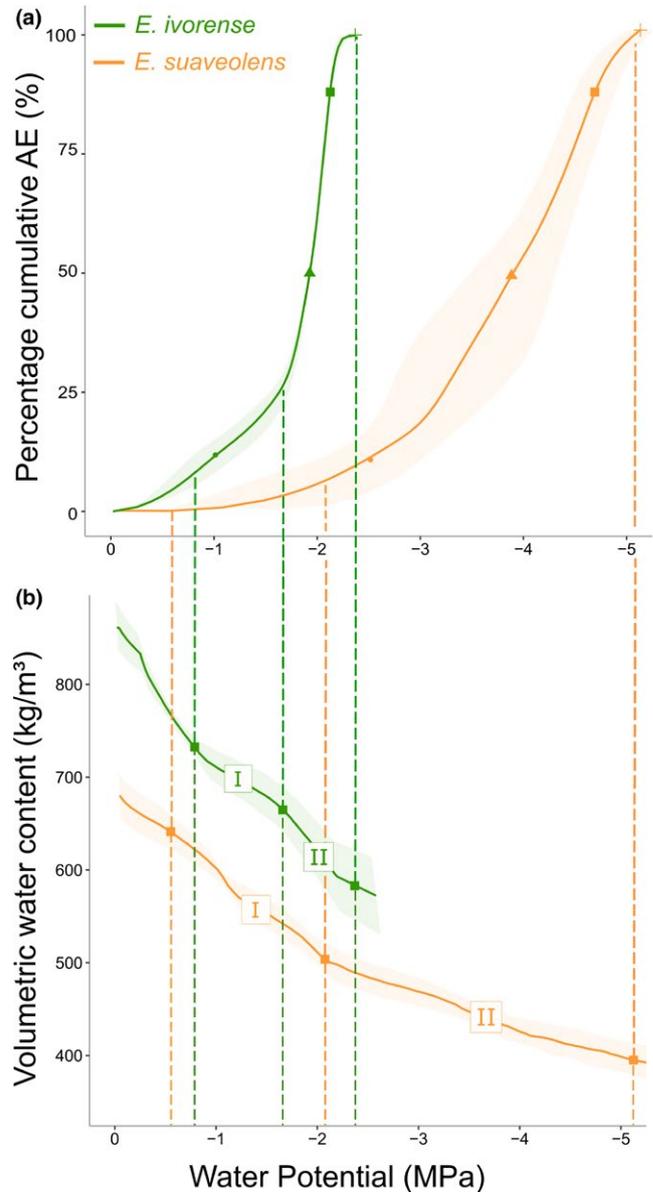
## 3 | RESULTS

### 3.1 | Hydraulic traits

The wet forest species, *E. ivorens*, was less resistant to drought-induced cavitation, with an average  $AE_{50} (\pm SD)$ , the 50% cavitation-related acoustic emission, of  $-1.93 \pm 0.03$  MPa (Figure 3a). The moist forest species *E. suaveolens* showed half the value of  $AE_{50}$  ( $-3.88 \pm 0.70$  MPa, Figure 3a). Branches were completely desiccated within  $1.88 \pm 0.02$  days for *E. ivorens* and  $3.73 \pm 0.56$  days for *E. suaveolens*.

Branches had an average ( $\pm SD$ ) initial volumetric water content (VWC) of  $861 \pm 65$  kg/m<sup>3</sup> for *E. ivorens* and  $680 \pm 20$  kg/m<sup>3</sup> for *E. suaveolens* (Figure 3b). As the dehydration progressed, the wet forest species, *E. ivorens*, was characterized by slightly lower elastic hydraulic capacitance ( $C_{el}$ , capacitance of phase I) compared to the moist forest species, *E. suaveolens* (respectively,  $68 \pm 22$  vs.  $94 \pm 32$  kg/m<sup>3</sup>/MPa,  $r^2 = 0.99$ , Figure 3b). In contrast, the inelastic capacitance ( $C_{inel}$ , capacitance of phase II) was four times higher for *E. ivorens* than for *E. suaveolens* ( $138 \pm 34$  vs  $35 \pm 14$  kg/m<sup>3</sup>/MPa,  $r^2 = 0.99$ , Figure 3b). The overall capacitance was higher for *E. ivorens* ( $108.72 \pm 1.68$  kg/m<sup>3</sup>/MPa,  $r^2 = 0.98$ ), than for *E. suaveolens* ( $51.48 \pm 1.25$  kg/m<sup>3</sup>/MPa,  $r^2 = 0.94$ ).

The amount of water released by the wet forest species *E. ivorens* is lower than that of the moist forest species, *E. suaveolens*. For *E. ivorens*, VWC decreased by 8% during the elastic phase and in total by 20% at the end of the inelastic phase (146 kg/m<sup>3</sup>), while for *E. suaveolens*, VWC decreased by 21% during the elastic phase and in total by 38% at the end of the inelastic phase (246 kg/m<sup>3</sup>, Figure 3b).



**FIGURE 3** Hydraulic traits. Acoustic vulnerability curves (a) and desorption curves (b) for the wet forest species *Erythrophleum ivorens* (green) and the moist forest species *E. suaveolens* (orange). Curves were computed on three individuals per species collected in their natural habitat. The average acoustic vulnerability curves with standard error margins ( $\pm SE$ ) were obtained by plotting cumulative AE values against xylem water potential. The vulnerability thresholds  $AE_{12}$  (circle),  $AE_{50}$  (triangle),  $AE_{88}$  (square), and  $AE_{100}$  (cross) are indicated as well. Desorption curves with standard error margins ( $\pm SE$ ) were obtained by plotting average volumetric water content against xylem water potential during the bench dehydration experiment. Phases I and II are delimited by vertical lines, and the slopes within these phases represent elastic ( $C_{el}$ ) and inelastic ( $C_{inel}$ ) hydraulic capacitance, respectively

### 3.2 | Wood traits

Given the strong differences in tree hydraulics between the two sister species (Figure 3), we further examined differences in wood anatomical traits, especially those related to hydraulic conduits

(Table 1). We identified some slight differences in wood traits, particularly in vessel-associated traits. In the natural habitat, *E. ivorens* showed a larger tangential vessel diameter, lower vessel density and vessel wall reinforcement, and larger diameter of intervessel pits compared to *E. suaveolens* (Figure 4a,b, Table 1). Other wood traits, including vessel grouping index, fiber wall thickness, and proportion of vessel, fiber, and parenchyma, did not differ between the species (Table 1). Differences in wood traits observed in the natural habitat were maintained in the common garden experiment (Figure 4c, Figure 1a, Table 1), arguing for a genotypic origin rather than environmental plasticity. Overall, vessel diameter and the proportion of

vessel lumen increased with distance to the pith for *E. ivorens* and *E. suaveolens* in both natural habitats and in the common garden experiment (Figure 4a,c, Table 1).

### 3.3 | Growth

The wet forest species *E. ivorens* had a faster inherent growth than *E. suaveolens* (Figure 5). For all diameters combined and in their natural habitat, the average diameter increment of *E. ivorens* was significantly higher than that of *E. suaveolens* ( $0.56 \pm 0.36$  cm/year vs.  $0.40 \pm 0.37$  cm/year, one-way ANOVA  $F$ -value = 6.74,  $p$ -value < 0.05,

**TABLE 1** Fixed parameter estimates, standard error (SE),  $p$ -values, and variance of the residuals ( $\sigma \epsilon_{ijsp}$ ) for the best linear mixed model for testing differences in wood traits between *Erythrophleum ivorens* (ivo) and *E. suaveolens* (sua)

	Wood traits	Parameter estimate $\pm$ SE	$p$ -value	$\sigma \epsilon_{ijsp}$
Branch in natural habitats	Vessel diameter ( $\mu\text{m}$ )	$a = 34.96 \pm 2.73$	<0.0001	16.32
		$b_{ivo} = 7.07 \pm 0.88$	<0.0001	
		$b_{sua} = 4.32 \pm 0.81$	<0.0001	
	Vessel density (per $\text{mm}^2$ )	$a = 56.51 \pm 8.27$	<0.0001	23.42
		$b_{ivo} = -1.25 \pm 2.96$	0.57	
		$b_{sua} = 7.89 \pm 3.48$	<0.05	
	Vessel grouping index	$a = 1.7 \pm 0.08$	<0.0001	0.65
	Vessel wall reinforcement ( $\mu\text{m}$ )	$a_{ivo} = 0.01 \pm 0.002$	<0.0001	0.17
		$a_{sua} = 0.02 \pm 0.002$	<0.001	
	Fiber wall thickness ( $\mu\text{m}$ )	$a = 5.33 \pm 0.21$	<0.0001	1.06
	Vessel lumen (%)	$a = 10.71 \pm 2.33$	<0.0001	5.68
		$b_{ivo} = 0.74 \pm 0.78$	0.35	
		$b_{sua} = 3.84 \pm 0.10$	< 0.001	
	Axial parenchyma (%)	$a = 31.67 \pm 4.78$	<0.0001	12.2
Radial parenchyma (%)	$a_{ivo} = 12.00 \pm 1.54$	<0.0001	4.27	
	$a_{sua} = 15.59 \pm 1.56$	0.055		
	$b = -1.35 \pm 0.49$	< 0.01		
Fiber (%)	$a_{ivo} = 50.01 \pm 6.09$	<0.0001	14.18	
	$a_{sua} = 52.46 \pm 7.16$	0.74		
	$b = -3.68 \pm 1.69$	<0.05		
Pit membrane diameter ( $\mu\text{m}$ )	$a_{ivo} = 7.03 \pm 0.20$	<0.001	0.92	
	$a_{sua} = 5.87 \pm 0.31$	<0.01		
Stem in natural habitats	Vessel diameter ( $\mu\text{m}$ )	$a_{ivo} = 229.50 \pm 10.44$	<0.001	54.05
		$a_{sua} = 190.93 \pm 17.35$	<0.05	
	Vessel density (per $\text{mm}^2$ )	$a = 3.28 \pm 0.25$	<0.0001	0.87
	Vessel grouping index	$a = 1.45 \pm 0.07$	<0.0001	0.17
	Vessel wall reinforcement ( $\mu\text{m}$ )	$a_{ivo} = 0.009 \pm 0.002$	<0.0001	0.009
		$a_{sua} = 0.017 \pm 0.003$	<0.05	
	Fiber wall thickness ( $\mu\text{m}$ )	$a = 9.16 \pm 0.40$	<0.0001	1.95
	Vessel lumen (%)	$a = 13.97 \pm 1.21$	<0.0001	1.77
	Axial parenchyma (%)	$a = 37.75 \pm 2.29$	<0.0001	6.41
	Radial parenchyma (%)	$a = 8.63 \pm 1.60$	<0.0001	3.36
	Fiber (%)	$a = 40.05 \pm 1.66$	<0.0001	11.71

(Continues)

**TABLE 1** (Continued)

	Wood traits	Parameter estimate ± SE	p-value	$\sigma \epsilon_{i sp}$
Branch in common garden	Vessel diameter (µm)	$a_{ivo} = 49.15 \pm 3.50$	<0.0001	14.5
		$a_{sua} = 38.71 \pm 4.21$	<0.05	
		$b = 6.35 \pm 0.55$	<0.0001	
	Vessel density (per mm <sup>2</sup> )	$a_{ivo} = 27.83 \pm 2.07$	<0.0001	13.66
		$a_{ivo} = 40.57 \pm 6.89$	0.091	
	Vessel grouping index	$a = 1.55 \pm 0.09$	<0.0001	0.92
	Vessel wall reinforcement (µm)	$a_{ivo} = 0.014 \pm 0.003$	<0.0001	0.011
		$a_{ivo} = 0.026 \pm 0.005$	<0.05	
	Fiber wall thickness (µm)	$a = 5.07 \pm 0.26$	<0.0001	0.92
	Vessel lumen (%)	$a = 7.75 \pm 1.67$	<0.0001	4.66
		$b_{ivo} = 0.55 \pm 0.56$	0.34	
		$b_{sua} = 1.83 \pm 0.62$	<0.01	
	Axial parenchyma (%)	$a = 17.11 \pm 2.10$	<0.0001	8.53
	Radial parenchyma (%)	$a = 20.39 \pm 2.87$	<0.0001	11.71
	Fiber (%)	$a = 46.34 \pm 2.91$	<0.0001	15.43

Notes. The model selection was based on the Akaike information criterion. For stem, model tested estimated wood trait (WT) of the individuals (*i*) belonging to each species (*sp*), with a random intercept ( $\alpha$ ):  $WT_{i,sp} = a_{sp} + \alpha_{i,sp} + \epsilon_{i,sp}$ . For branch, the effect of the distance to the pith (*dist*) and a random slope ( $\beta$ ) have been added in order to consider radial variation in wood anatomy:  $WT_{i,sp} = a_{sp} + b_{sp} \times dist + \alpha_{i,sp} + \beta_{i,sp} \times dist + \epsilon_{i,sp}$ ; with  $a_{sp}$  and  $b_{sp}$  as fixed parameters,  $\alpha_{i,sp}$  and  $\beta_{i,sp}$  as random parameters, and  $\epsilon_{i,sp}$  as the random error.

Figure 5a). Although *E. ivorens* was under-represented in diameter classes lower than 40 cm and higher than 80 cm, the faster growth of *E. ivorens* was mainly maintained when size/ontogeny was taken into account (Figure 5b). In the common garden experiment, the growth difference between the two species was maintained and strengthened ( $2.59 \pm 0.92$  cm/year for *E. ivorens* vs.  $1.63 \pm 0.64$  cm/year for *E. suaveolens*, one-way ANOVA *F*-value = 78.62, *p*-value < 0.001, Figure 5c). Thus, juvenile trees of *E. suaveolens* did not exhibit any home advantage in terms of growth. The two species grew faster in the common garden experiment, probably due to the absence of competitors and higher light availability in the plantation.

### 3.4 | Life-history traits

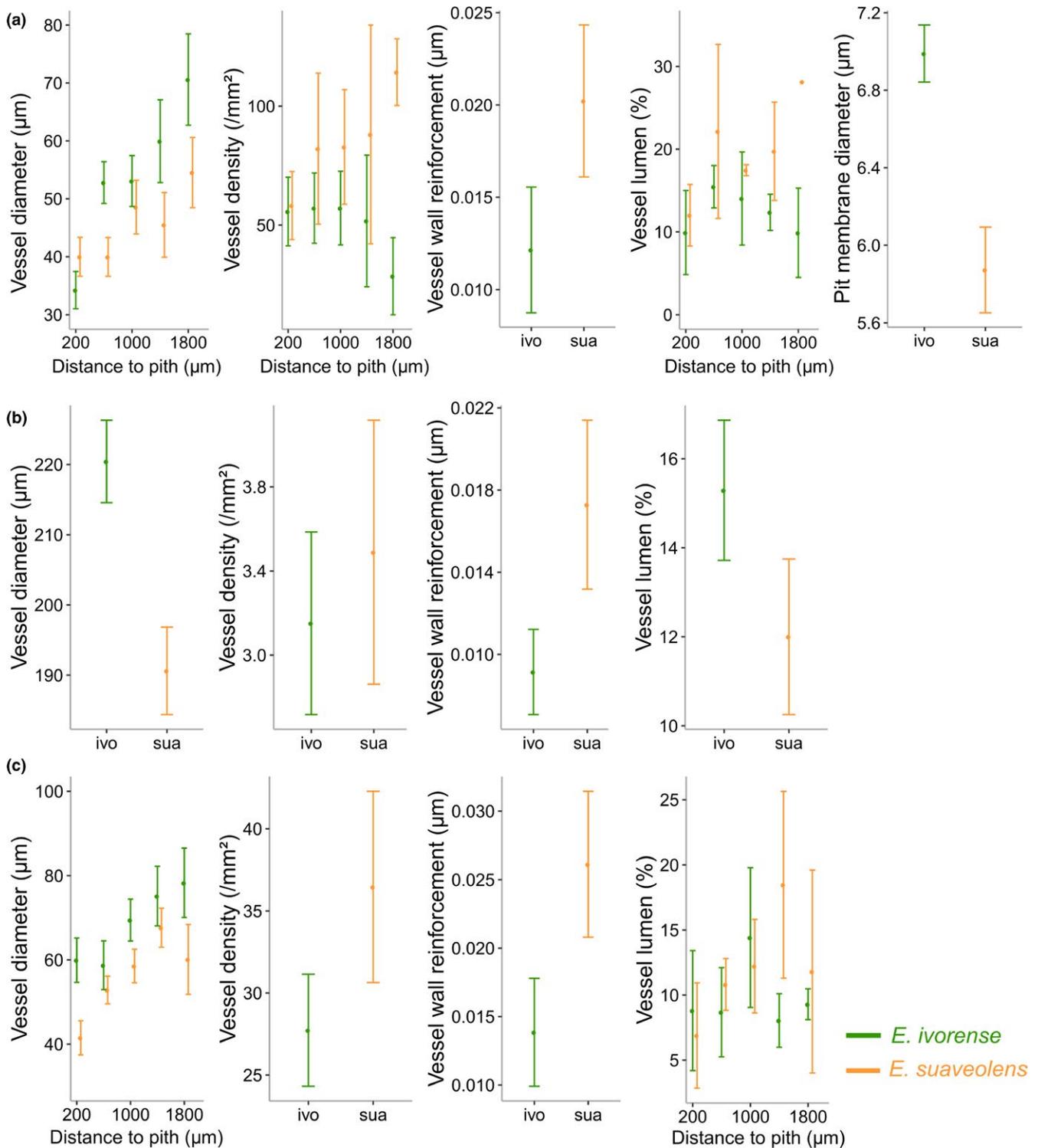
Wood density of the wet forest species *E. ivorens* tended to be lower than that of the moist forest species, *E. suaveolens* (Table 2). The  $CEI_{juv}$ , which approximate light requirements at juvenile stage, was higher for the wet forest species *E. ivorens* than for the moist forest species *E. suaveolens* (2.14 vs. 1.57) and reflected the establishment of *E. ivorens* in higher light conditions. Finally, the average ( $\pm$ SD) seed mass of *E. ivorens* was twice lower than that of *E. suaveolens* ( $1.46 \pm 0.26$  g vs  $3.02 \pm 0.26$  g).

## 4 | DISCUSSION

Tropical tree species distribution along rainfall gradients and underlying drought response strategies, hydraulics, and wood anatomical traits have previously been examined (Engelbrecht et al.,

2007; Gaviria & Engelbrecht, 2015; Gaviria, Turner & Engelbrecht, 2017; Maharjan et al., 2011; Poorter & Markesteijn, 2008; Sterck, Markesteijn, Toledo, Schieving & Poorter, 2014), but not necessarily on closely related species (but see Pfautsch et al., 2016; for *Eucalyptus*). In this study, we examined how tree species evolved on a rainfall gradient with an integrated eco-physio-morphological approach. Our two species, *E. ivorens* and *E. suaveolens*, broadly share the same general wood anatomical features (InsideWood 2004) and are hard to distinguish in the field, though genetic studies showed contrasted distributions. Here, we identified some slight differences in wood traits that resulted in strong differences in tree hydraulics, growth, and overall species distribution. The conserved between-species differences in wood trait and growth in the natural habitat and in the common garden argue for a genotypic origin rather than environmental plasticity as discussed by Pfautsch et al. (2016). We cautiously interpret these differences as reflecting a long-term adaptation to drought.

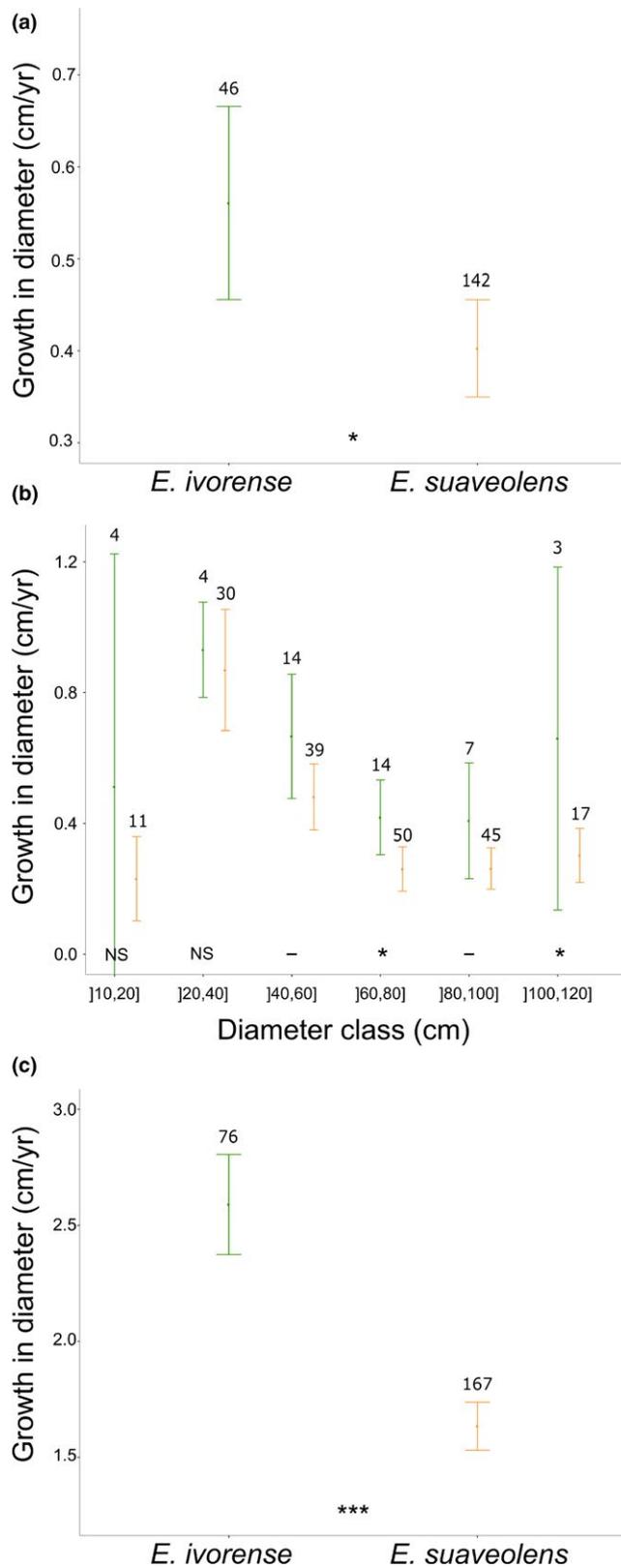
As expected, the wet forest species, *E. ivorens*, had lower resistance to cavitation than the moist forest species, *E. suaveolens*. The tension at which the xylem experiences 50% loss of conductivity ( $\psi_{50}$  or the equivalent  $AE_{50}$  in the acoustic method) is usually used as a benchmark for species comparison (Anderegg, 2015). For the wet forest species *E. ivorens*, the average  $AE_{50}$  value of  $-1.9 \pm 0.1$  MPa reported here is similar to that reported by Markesteijn, Poorter, Bongers, Paz, and Sack (2011), Markesteijn, Poorter, Paz, Sack, and Bongers (2011) for pioneer saplings ( $-1.8 \pm 0.4$  MPa), in line with its high light requirement. The moist forest species, *E. suaveolens*, was less vulnerable, with a lower  $AE_{50}$  of  $-3.9 \pm 0.5$  MPa. Following Choat et al. (2012), such a value indicates low vulnerability to



**FIGURE 4** Wood traits. Average of vessel diameter, vessel density, vessel wall reinforcement, percentage of vessel lumen and intervessel pit diameter (only for branches collected in the natural habitat), and 95% confidence intervals for branches ( $n = 5$ ) and stem ( $n = 5$ ) collected in the natural habitat (respectively, a and b) and for branch samples ( $n = 5$ ) collected in a common garden experiment (c) for the wet forest species *Erythrophleum ivorense* (green) and the moist forest species *E. suaveolens* (orange)

drought-induced cavitation, with only 10% of the tropical tree species sampled worldwide showing lower vulnerability. Resistance to cavitation in the *Erythrophleum* genus appeared to be mainly controlled by differences in vessel characteristics. The higher resistance to cavitation of the moist forest species, *E. suaveolens*, was

associated with shallower intervessel pit chambers and smaller vessel diameters, which have the benefit of minimizing cavitation risk (Lens et al., 2011; Li et al., 2016), but reduce hydraulic conductivity (Choat, Brodie, Cobb, Zwieniecki & Holbrook, 2006; Wheeler, Sperry, Hacke & Hoang, 2005).



**FIGURE 5** Individual performance. Average growth and 95% confidence intervals of the wet forest species *Erythrophloeum ivorense* (green) and of the moist forest species *E. suaveolens* (orange) in the natural habitat (a), in natural habitat by diameter classes (b), and in the common garden experiment (c). Significance of the one-way ANOVA tests is given, with NS:  $p$ -value > 0.1, -:  $p$ -value < 0.1, \*:  $p$ -value < 0.05, and \*\*\*:  $p$ -value < 0.001. Number of individuals is given above each line range

species to buffer increases in xylem tension (Anderegg & Meinzer, 2015; Sperry et al., 2008) and to limit embolism formation (Phillips, Oren, Licata & Linder, 2004). As previously reported for tropical trees, we found that the species with the lowest resistance to cavitation and the lowest wood density, that is, the wet forest species *E. ivorense*, also showed the highest wood volumetric water content (Borchert, 1994) and the highest overall hydraulic capacitance (Borchert, 1998; Borchert & Pockman, 2005; Mcculloh, Johnson, Meinzer & Woodruff, 2014; Meinzer, James, Goldstein & Woodruff, 2003; Oliva Carrasco et al., 2015). Notwithstanding these points, during desiccation, the amount of water released by the moist forest species, *E. suaveolens*, is higher ( $246 \text{ kg/m}^3$ ) than that of the wet forest species, *E. ivorense* ( $146 \text{ kg/m}^3$ ). Associated with strong embolism-resistant xylem conduits, this contributed to the delay for complete dehydration (four days) in *E. suaveolens* while it took less than two days in *E. ivorense*. Undoubtedly, these two hydraulic strategies confer an adaptive value under drought episodes of different intensity and/or duration. During short dry periods, the high hydraulic capacitance of *E. ivorense* allows avoiding a large percentage of embolism formation in the xylem (Oliva Carrasco et al., 2015). During intense and longer drought periods, the strong cavitation resistance of *E. suaveolens*, associated with a continuous internal water supply of the xylem, contributes to a higher fitness (Sperry et al., 2008).

The computation of hydraulic capacitance for the elastic and the inelastic phases allowed us to investigate the fine-scale mechanisms of internal water transfer (Vergeynst, Dierick, et al., 2015) and was complemented by detailed analysis of associated wood traits. The elastic phase (and the related capacitance,  $C_{el}$ ) occurs when water is released from the elastic shrinkage of living cells. In contrast, the inelastic phase (and  $C_{inel}$ ) occurs when cavitation is strong and water is released from embolized conduits into the still functional ones. The wet forest species, *E. ivorense*, was characterized by a lower  $C_{el}$  compared to the moist forest species *E. suaveolens* (respectively,  $68 \pm 22$  vs  $94 \pm 32 \text{ kg/m}^3/\text{MPa}$ ), and a four times higher  $C_{inel}$  value ( $138 \pm 34$  vs  $35 \pm 14 \text{ kg/m}^3/\text{MPa}$ ). During the elastic phase, the role of the parenchyma in refilling conduits has mainly been invoked (Borchert & Pockman, 2005; Brodersen & McElrone, 2013; Morris & Jansen, 2016). Contrary to expectation, we did not find a positive link between  $C_{el}$  and the proportion of axial and/or radial parenchyma. But it is possible that the water stored in other tissues, such as bark and pith, contributes to  $C_{el}$  (Wolfe & Kursar, 2015). The higher  $C_{inel}$  for the wet forest species, *E. ivorense*, might be attributed to the larger vessels compared to those of the moist forest species. Indeed, because the vessels are inherently larger, the amount of water released from one embolized vessel is expected to be higher. At the same

In addition to the relatively classical drought-induced cavitation, we also examined hydraulic traits that are often-neglected: wood volumetric water content and hydraulic capacitance (Epila, Maes, et al., 2017; Vergeynst, Dierick, et al., 2015). These traits, which are involved in desiccation delay strategies, determine the capacity of a

**TABLE 2** Light requirement and life-history traits for the wet forest species *Erythrophleum ivorense* and for the moist forest species *E. suaveolens* ( $CEI_{juv}$  corresponds to the crown exposure index at 10 cm)

	<i>E. ivorense</i>	<i>E. suaveolens</i>
$CEI_{juv}$	2.14	1.57
Seed mass (g)	1.46 ± 0.26	3.02 ± 0.26
Wood density (g/cm <sup>3</sup> ) from the Global Wood Density Database (Zanne et al., 2009)	0.77 ± 0.06	0.82 ± 0.03
In situ branch wood density (g/cm <sup>3</sup> )	0.49 ± 0.04	0.58 ± 0.05
Common garden branch wood density (g/cm <sup>3</sup> )	0.50 ± 0.04	0.49 ± 0.03

time, the higher vessel density of the moist forest species, *E. suaveolens*, enables the embolism of a higher portion of conduits to safeguard the still functional ones. The production of many small vessels could be advantageous in drier environments, because a large proportion of small vessels can serve as a water reservoir to mitigate drought-induced xylem tension, in addition to the greater resistance to cavitation (Zanne et al., 2013).

When examining more classical functional traits for tropical tree species, the wet forest species, *E. ivorense*, showed characteristics of a fast growing species, with a high light demand (high  $CEI_{juv}$ ) and small seeds (Myers & Kitajima, 2007; Westoby, 1998). In contrast, the moist forest species, *E. suaveolens*, showed traits indicative of a better adaptation to stressful understory conditions at the juvenile stage. The light demand of the wet forest species, *E. ivorense*, was similar to values reported by Poorter and Kitajima (2007) for tropical pioneers while that of the moist forest species, *E. suaveolens*, was indicative of partial shade tolerance (Sheil et al., 2006). Seed mass is an important component of the life-history strategy (Westoby, 1998). The seed mass of the wet forest species was half that of the moist forest species. Fast growing species tend to have smaller seeds, while species with larger seeds survive better under drought and shaded conditions (Moles & Westoby, 2006; Westoby, 1998). These results point toward a coordinated drought and shade tolerance of *E. suaveolens* and do not support for a trade-off between shade and drought tolerance as proposed by Brenes-Arguedas, Coley and Kursar (2009) for 24 tropical tree species across the Isthmus of Panama.

Finally, the faster growth of wet forest species has previously been observed in Panama (Brenes-Arguedas et al., 2009; Gaviria & Engelbrecht, 2015; Gaviria et al., 2017) and in Bolivia (Markesteyn & Poorter, 2009). Here, the fast growth of the wet forest species was related to wood traits allowing a high hydraulic conductivity (Anderegg & Meinzer, 2015; Sperry et al., 2008; Tyree, Davis & Cochard, 1994) which could in turn maintain high transpiration and photosynthetic rates (Santiago et al., 2004). These wood traits, however, confer sensitivity to embolism and overall drought sensitivity (Markesteyn, Poorter, Bongers, et al., 2011; Tyree et al., 1994). In contrast, the slow growth rate of the drought-tolerant moist forest species, *E. suaveolens*, has been interpreted as the cost resulting from stress adaptation (Smith & Huston, 1990). The specialization to drier environments promotes wood traits that result in lower vulnerability to drought-induced cavitation at the cost of reduced water transport efficiency (Sperry et al., 2008) and lower growth rate (Gaviria & Engelbrecht, 2015; Polley, Tischler, Johnson & Derner, 2002).

Our results confirm a trade-off between drought tolerance and growth, controlled by subtle adaptations in wood traits, as a key mechanism leading to the niche partitioning between the two *Erythrophleum* species. The low drought tolerance of the wet forest species, *E. ivorense*, likely explains the exclusion from the moist and seasonal forests (Currie et al. 2004). In contrast, the high drought tolerance of the moist forest species, *E. suaveolens*, due to the combined action of a low vulnerability to cavitation and a desiccation delay strategy, seems to be associated with a low growth rate and certainly with a competitive exclusion from wet forests (Gaviria & Engelbrecht, 2015; Gaviria et al., 2017; Markesteyn & Poorter, 2009). The importance of this trade-off in the diversification of the African tree flora remains to be tested and an integrated eco-physio-morpho approach linking wood anatomy, hydraulics, growth, and distribution, as developed here could be the way forward.

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#### DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hj0005k> (Gorel et al., 2019).

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## SUPPORTING INFORMATION

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